

# CEPHALASPIDS FROM THE LOWER DEVONIAN OF PRINCE OF WALES ISLAND, CANADA

by D. L. DINELEY

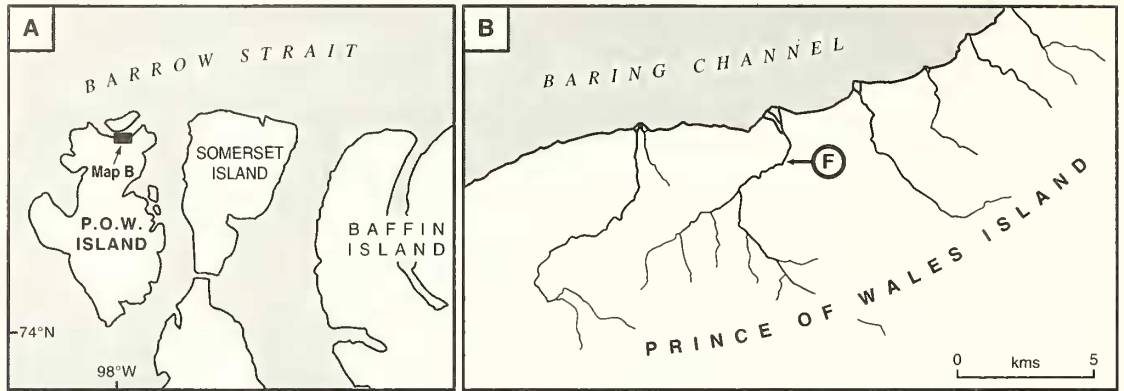
**ABSTRACT.** A Lochkovian vertebrate assemblage from the Peel Sound Formation of northern Prince of Wales Island, Northwest Territories, Canada, includes numerous headshields resembling the osteostracan *Parameteoraspis*, together with several fragments suggesting *Machairaspis*. Five specimens of the former, distinct in their extended and diverging pectoral cornua, may be regarded as a conspecific variety. A possible advantage afforded by such cornua, in this and other species, may be their use in swimming and in disturbing the substrate during feeding. A similar role for the rostra of other osteostracans and eugaleaspids is suspected.

THE Silurian and Devonian vertebrate-bearing rocks of Arctic Canada lie within Young's (1981) Euramerican or Cephalaspid vertebrate province of the Lower Devonian. Cephalaspids, as the distinguishing element in the faunas, occur widely throughout the province, and constitute a diverse but puzzling group. They are conspicuous though not abundant in the Downtonian and Dittonian Series in the British Isles and Western Europe (Stensiö 1932; Heintz 1940; White 1961, 1985), Svalbard (Wängsjö 1952; Janvier 1985*a*) and Podolia (Janvier 1985*b*, 1988). Osteostraci appear to have little stratigraphical value in much of the Euramerican Province. Only in Spitsbergen has it been possible to plot their stratigraphical ranges on the basis of common, if not abundant, material within the Red Bay and Wood Bay formations (Janvier 1985*a*), which are Přídolí to Lochkov in age.

On the North American mainland they are relatively less abundant but are known from the Atlantic area (Robertson 1936; Dineley 1967; Pageau 1969) and from several places in the southwestern States (Denison 1952). From northern Canada they have been recorded from a very few localities on Somerset Island (Dineley 1968) and from the MacKenzie Mountains (Dineley and Loeffler 1976). In all these vertebrate 'communities' the Osteostraci occupy a comparatively minor role, being neither abundant nor taxonomically diverse in comparison with the other members. The material described here, however, comes from a small volume of rock in which the cephalaspids are relatively common within a very restricted assemblage or faunule, which presumably may represent a similar 'community'. The state of preservation is poor, making taxonomic identification difficult, but this does not obscure the wide variation in the shape of the headshield in what is here regarded as a single species.

## LOCALITY AND FAUNA

The cephalaspid-yielding horizon on Prince of Wales Island lies relatively high in the sandstone-carbonate facies of the upper member of the local Peel Sound Formation. This unit is essentially confined to the vicinity of the Boothia Uplift where the Silurian to Devonian succession exhibits proximal Old Red Sandstone facies passing laterally into distal marine carbonates and minor clastics (Miall 1970). Stewart (1987) has given an overall account of the stratigraphy of the region, noting the occurrence of vertebrates in the marine facies of the Ludlovian and Přídolí and also in the non-marine rocks of the Peel Sound Formation. Dineley (1990) has outlined the vertebrate palaeontology, drawing attention to the scattered but very numerous localities at which vertebrate remains occur. On the basis of both agnathan and gnathostome vertebrates and the invertebrates, Elliott (1984) broadly correlated the horizon from which the present fauna comes



TEXT-FIG. 1. A, part of Northwest Territories, Canada, with the position of Text-figure 1B indicated. B, the cephalaspid-yielding locality (F) in northern Prince of Wales Island.

with the *vogti* Horizon in Spitsbergen, with the lower part of the *crouchi* Zone in Britain and with the Czortkow Horizon in Podolia. This is within the Lochkovian Stage.

The locality is on the east bank of a small water-course near the north coast (the Baring Channel) of Prince of Wales Island (F on Text-fig. 1, and given as locality A in Dineley 1976, p. 2). Here a green-weathering fine sandstone contains:

<i>Ctenaspis obruchevi</i> Dineley	common
Cyathaspid indet. cf. <i>Pionaspis</i>	rare
? <i>Baringaspis dineleyi</i> Miles	very rare
? <i>Parameteoraspis</i> cf. <i>P. oblonga</i> (Wängsjö)	common
Cephalaspid indet. cf. <i>Machairaspis</i> sp.	very rare

Virtually all the fossils are fragmentary or isolated headshields, portions of cephalaspid, and other squamation and minor indeterminate debris. Several *Ctenaspis* and cephalaspid headshields bear attached squamation; the former include complete trunk and tail parts (Dineley 1976). The dorsal and ventral *Ctenaspis* shields are separated and the scales seem to be attached to the dorsal shields only. These remains have been water-transported, presumably soon after the death of the animals and before complete disintegration took place. As is the case in virtually all cephalaspid occurrences, the headshields appear to be the right way up. No marine invertebrate fossils accompany the vertebrates and a freshwater or brackish environment of deposition is possible. There are no microvertebrates. The assemblage seems to represent a single benthonic, if not infaunal, community, together with the active nektonic arthrodire *Baringaspis*. It is unique amongst the many vertebrate-bearing levels in the vicinity of the Boothia Uplift in the relatively large number of cephalaspid individuals present: in all other assemblages Osteostraci are very rare.

#### SYSTEMATIC PALAEOLOGY

Order OSTEOSTRACI Lankester, 1868

Suborder CORNUATA Janvier, 1985a

Family Group CEPHALASPIDIENS Janvier, 1985a

GENUS PARAMETEORASPIS Blicek *et al.*, 1987

*Type species.* *Cephalaspis gigas* Wängsjö, 1952.

TABLE 1. Measurements (in mm) of cephalaspid headshields from the locality near Baring Channel, Prince of Wales Island. A, length of median from rostral margin to level of cornual tips; B, distance between cornual tips; C, distance between median point of rostral margin and cornual tip; \*, form with elongate and divergent cornua. Number of specimens measured = 21.

Spec. No.	A	B	C	A/B
12471	48	52	—	0.92
12474	—	62	56	—
12476	75	55	—	1.36
12477*	—	67	72	—
12478	—	59	61	—
12480	50	70	—	0.71
12481	—	62	62	—
12482	55	64	62	0.85
12483	42	65	64	0.64
12484*	—	70	72	—
12487	—	70	66	—
12488	55	60	61	0.91
12489	50	70	66	0.71
12496	58	65	64	0.89
12497	—	65	64	—
12498	—	69	52	—
12501	52	62	—	0.83
12503	40	60	—	0.66
12504	—	72	68	—
12506*	64	77	82	0.83
12511	58	69	66	0.60
Average (typical)	53	60	68	—
Mean	57.5	61	60	—
Range				0.60–0.92

*Parameteoraspis* cf. *P. oblonga* (Wängsjö, 1952)

Plate 1, figures 1–6, Text-figure 2A–E

*Material.* Fragmentary head shields, some with adjacent squamation; Canadian Museum of Nature, Ottawa, NMC 12471–12498, NMC 12501–12506, 12511.

*Locality and horizon.* Stream bank near north coast of Prince of Wales Island, arctic Canada; Lochkovian, Lower Devonian.

*Description.* The bulk of the osteostracan material (Pl. 1; Text-fig. 2A–E) appears to belong to a medium-size true cephalaspid, tentatively compared below to *Parameteoraspis oblonga* (Stensiö). In addition, two other fragments of cephalaspid head shield bear relatively large orbits and traces of a large medial spinal crest such as is found in *Machairaspis*.

Some twenty-five specimens preserve most of the outline of a cephalaspid head shield in dorsal or ventral aspect. While the outline of each is intact, it has not been possible to distinguish much of the detailed morphology, such as sensory fields, nerve or vascular canals, or the positions of the nasal, pineal or orbital apertures. The bone itself is very thin and has been severely crushed. Additionally, vertical compression of the head shield has deformed the median profile. No external ornamentation has been observed.

The dimensions are given in Table 1. The size range is small and the animals were presumably all of the same generation or approximate age. Size was regarded as a specific character by Stensiö (1932) and by Wängsjö (1952). White (1985), however, noted as much as two hundred per cent variation in some British species.

The fossils represent a group of medium-size cephalaspidids *sensu stricto* (Cephalaspidiens of Janvier 1985a) with very prominent pectoral cornua that lack marginal denticles. The rim of the headshield varies little in shape, except in five individuals. The majority exhibit a smooth parabolic curve from the rostral median point to the cornua. There is no rostral lip, process or thickening of the rim. The pectoral cornua are broad and directed posteriorly or postero-laterally. They appear to have been originally thin or flat and subsequently further dorso-ventrally compressed. The pectoral sinus is rather narrow to broad and the interzonal part of the shield extends backwards to almost half the length of the cornua. As is normal in the cephalaspids, the ventral surface of the head is flat; the dorsal is domed to a height of about 15 mm in the posterior median part but with wide flat margins. In plan view, the general outline with broad-based cornual processes is similar to *Cephalaspis lyelli* Agassiz (White 1958).

Such evidence as there is of the original dorsal surface suggests that the lateral fields were probably inconspicuous, long and narrow, extending well into the cornual regions. The size, position and shape of the central sensory field are obscure, but the orbits are small, situated high, about halfway back from the anterior margin and just in front of the presumed position of the central field. Neither nasal nor pineal apertures have been identified. Poor preservation also precludes the recognition of dorsal surface ornamentation, nor has any trace of the features of the ventral surface survived (Plate 1). Thus it has not been possible to determine if tuberculation (a diagnostic character) was originally present. Several specimens (NMC 12476, 12489, 12500, 12504, 12506B, for example) retain impressions or fragments of the scale rings immediately behind the headshield. The scales are similar to those of other cephalaspids, being narrow and tall, with appreciable overlap posteriorly. So far, no vestige of a large median dorsal scute, as present in the true cephalaspidians, has been found. No sign of pectoral appendages is seen.

Five head shields (NMC 12476, 12482, 12484, 12497, 12506) differ from the majority in dorsal view, having broadly divergent cornua (Text-fig. 2c). The median length is about 45 mm but the points of the cornua are some 80 mm apart. The anterior margins of these specimens are broadly rounded with no apical angle or rostral feature, the lateral margins are straight almost to the hind tip. Thus the cornua are directed posterolaterally, as in such species as *Parameteoraspis caroli* (Wängsjö). The pectoral sinus is wide and short. *P. caroli* is a larger cephalaspid, being some 60 by 18 mm in size. As far as can be seen, all other features in these five specimens correspond to those in the remainder. Such a marked difference in outline of the head shield has been used as a specific character by previous authors, and at least four such species have been described from the Wood Bay Formation of Spitsbergen (Janvier 1985a) where there are big size differences between the species. It is not proposed to raise the present specimens to higher taxonomic rank than variety here.

On the meagre evidence from this material there is no obvious taxon to which it may be referred. It nevertheless seems to be close to the species *Parameteoraspis oblonga* (Stensiö). The genus contains species both larger and smaller in size than that of the present specimens. It is now recorded also from the Lower Emsian 'Klerfer Schichten' of the Rheinisches Schiefergebirge (Bardenheuer and Janvier, 1990).

*Discussion.* Janvier (1981; 1985a p. 200) defined *Parameteoraspis* (under its previous invalid name *Meteoraspis*) thus:

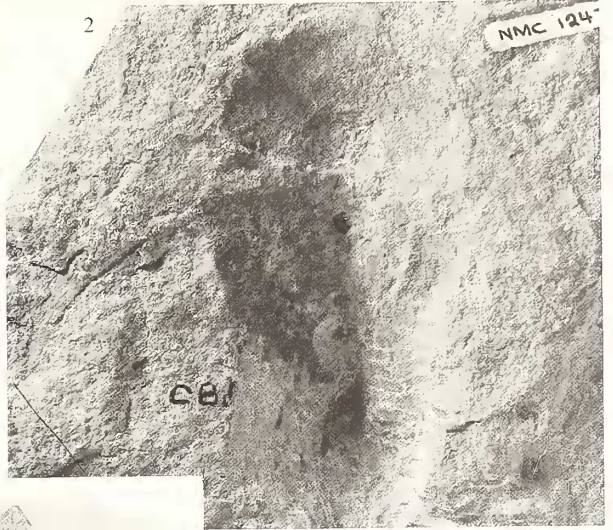
Cephalaspidians of generally large size; cornual processes long and proximally wide, bearing the posterior part of the lateral fields, which is narrow and follows the lateral borders of the cornua almost to their ends. The median dorsal field is also wide and short, including the external openings of the endolymphatic ducts. The pineal plate is replaced by separate tesserae of the same kind as those covering the median dorsal field. The naso-hypophysial opening is an elongated slit. The superficial layer of the exoskeleton is continuous in mature individuals, but is smooth except around the orbits and along the margins of the shield, where it carries very small irregular tubercles.

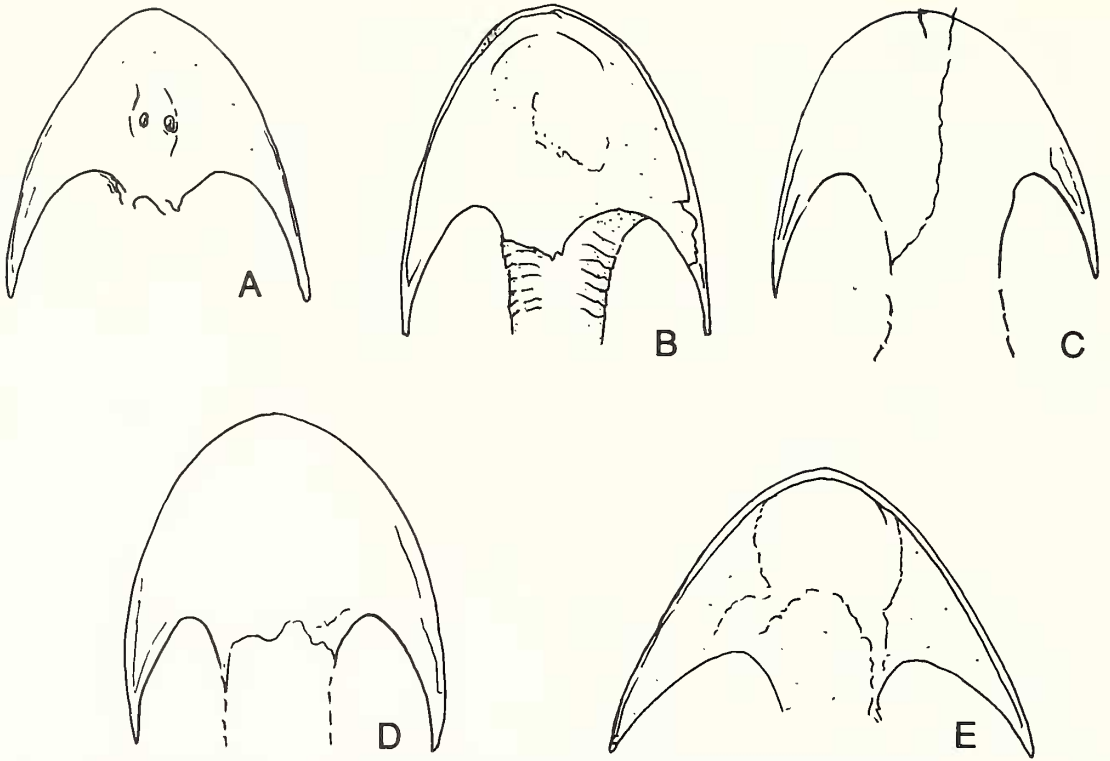
His (emended) diagnosis of Wängsjö's (1952) species *M. oblonga* (Stensiö) reads:

*Meteoraspis* of medium dimensions, shield longer than broad, with parabolic rostral margin and cornual processes directed posteriorly. Spinal crest present but projecting only slightly.

#### EXPLANATION OF PLATE I

Figs 1–4. ?*Parameteoraspis* cf. *oblonga* (Stensiö); Figs 5–6. ?*Parameteoraspis* cf. *oblonga* var. All from the Peel Sound Formation of northern Prince of Wales Island, Canada. 1, NMC 12482a; 2, NMC 12476; 3, NMC 12506b; 4, NMC 12483; 5, NMC 12488; 6, NMC 12489. All figures *c.* × 1.





TEXT-FIG. 2. ?*Parameteoraspis* cf. *oblonga* (Stensiö) from the Upper Member of the Peel Sound Formation, northern Prince of Wales Island, Canada; poorly preserved cephalic shields with traces of squamation. A, NMC 12483; B, NMC 12489; C, NMC 12474; D, NMC 12487; E, NMC 12506. All figures *c.*  $\times 0.6$ .

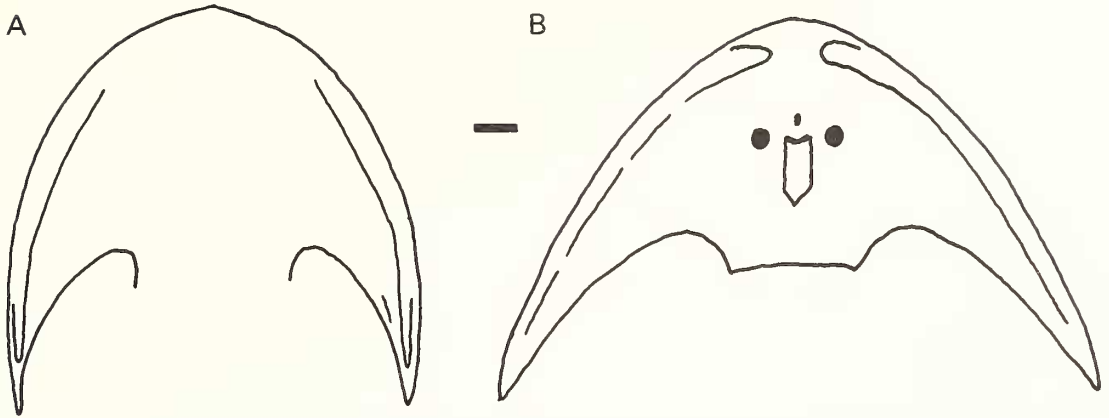
There is little new material to amplify the original diagnoses, which nevertheless approximate more closely than others to the present specimens (Text-fig. 3). The Prince of Wales Island material shows no trace of tubercles on the marginal surface nor of a spinal crest.

The five specimens with laterally extended cornua conform generally with these criteria except for the diverging axes of these features. Their appearance in an otherwise uniform sample of a species of cephalaspid suggests that they may embody a response to a particular environmental opportunity. It may follow that should the opportunity have persisted the response may have led to the establishment of a separate species of which these few individuals were possibly the forerunners. So far no further cephalaspids have been found at higher levels in this facies, nor have such distinctively cornuate forms been found elsewhere in this region.

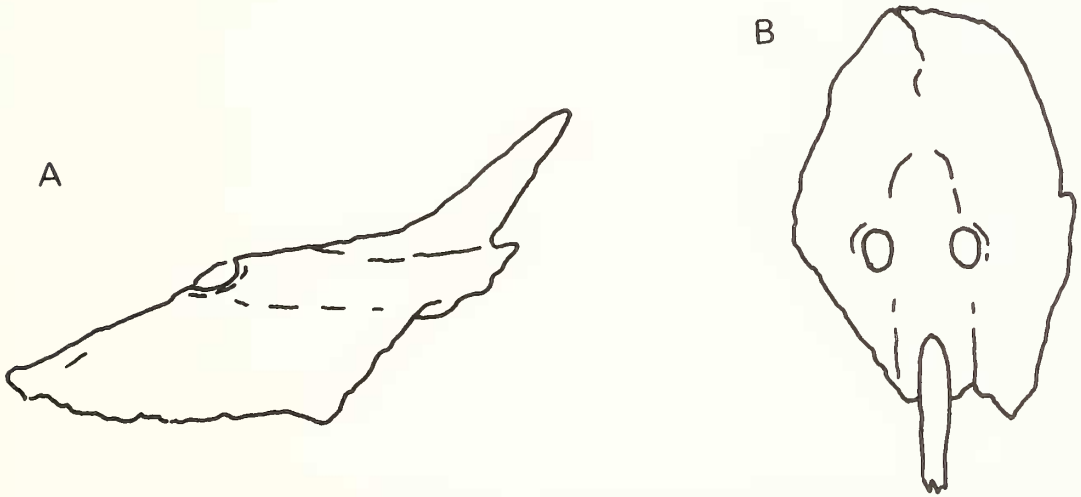
The four or more Spitsbergen species with widely divergent pectoral cornua have been described from rather sparse material. Their characteristics generally, however, are distinct, whereas the Canadian specimens are distinguished from the more numerous individuals present only by their pectoral width.

#### Genus MACHAIRASPIS Janvier 1985a

*Type species.* *Cephalaspis corystis* (Wängsjö, 1952)



TEXT-FIG. 3. A, *Parameteoraspis oblonga* (Stensiö). B, *Parameteoraspis caroli* (Wängsjö). Both figures are after Janvier (1985). Scale bar represents 10 mm.



TEXT-FIG. 4. Cephalaspid indet. cf. *Machairaspis*. A-B, NMC 12517; left lateral and dorsal views;  $c. \times 1$ .

cf. *Machairaspis* sp.

Text-figure 4A-B.

*Material.* Two fragments of cephalaspidian head shield bearing the basal part of a median dorsal spine or vane (NMC 12517, 12534).

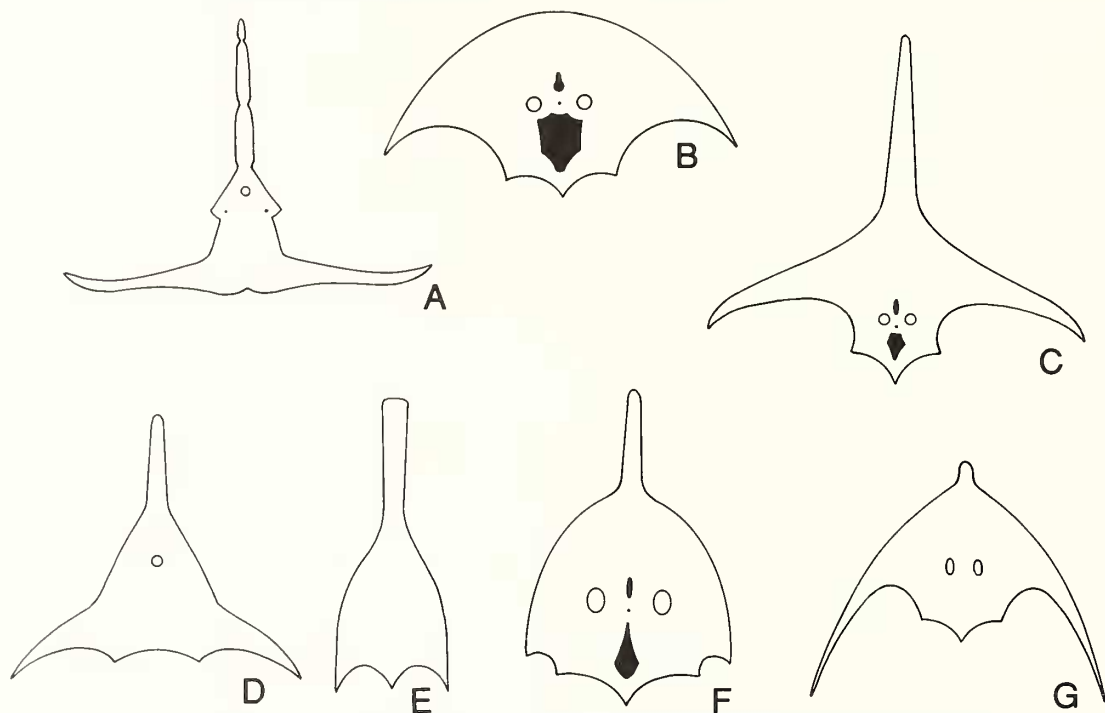
*Locality and horizon.* As for *Parameteoraspis* cf. *P. oblonga*. In Spitsbergen *Machairaspis* ranges throughout the Fraenkelryggen and Ben Nevis Formations into the Kapp Kjeldsen Division of the Wood Bay Formation; it therefore extends from the Lochkovian into the lower Pragian.

*Description.* The presence of fragments of osteostracan headshields with a median spinal process indicates the presence of another genus. Genera bearing a dorsal spine or vane are few and rare. The zenaspidians (scolenaspidians of Janvier 1985a, p. 116) *Scolenaspis* and *Machairaspis* are the prime examples. The material from Prince of Wales Island represents a form somewhat larger than *Parameteoraspis*, but generally small compared with the Spitsbergen species. No surface ornament or tuberculation is apparent. The orbits are large

and set high on the shield; the leading edge of the spinal process is strongly inclined to the posterior, but specimen NMC 12517 is deformed and identification as *Machairaspis* is most tentative.

*Discussion.* Although the variety of wide headshield is represented by only five specimens, they are of constant proportions and do not seem to be deformed or misshapen in any significant way. They may represent a form that may have been at no disadvantage in competition with the *forma typica*.

The headshield itself is an almost complete rigid box of bone; only its floor between mouth, branchial openings and the abdominal exoskeleton, was in any way flexible. This, and the mouthparts, were required to move during feeding and respiration. The general structure of cephalaspids is consistent with a benthonic mode of life wherein the development of pectoral glide planes may have assisted in lift-off from the bottom when required for feeding and breathing and especially during locomotion. Pectoral appendages would effectively provide additional and directional drive. Belles-Isles (1987) has analysed swimming modes and hydrodynamics for two agnathan species, *Alaspis macrotuberculata* and *Pteraspis rostrata*.



TEXT-FIG. 5. Late Silurian and Early Devonian Agnatha with both long pectoral cornua and long rostra. A, *Lungmenshanaspis*; B, *benneviaspid*; C, *Boreaspis*; D, *Sanqiaspis*; E, *Asiaspis*; F, *Spatulaspis*; G, *Dicranaspis*. A, E, G, from South China; B-D, F, from Spitsbergen. Figures not drawn to scale.

The late Devonian osteostracan *Alaspis* is morphologically similar to *Parameteoraspis*, and although no pectoral appendages have yet been discovered in the latter, it may be assumed that the two species functioned in similar fashion. Janvier (1985a, p. 225) and Belles-Isles (1987) considered that in the Boreaspidae the extended rostral and pectoral processes may have had a defensive function against predators. It is, however, hard to see how extended cornua would have given a defensive advantage. Their hydrodynamic function is still not fully understood. Belles-Isles (1987, p. 367) emphasized the role of cornua in increasing manoeuvrability, and noted that the environment was frequently turbulent. Janvier's (1985a) cladistic analysis of the Spitsbergen osteostraci draws a fundamental division between cornuate and non-cornuate taxa. The latter are



the earlier (Silurian) forms; the cornuates include his groups cephalaspidiens, thyestidiens, scolenaspidiens, kiaeraspidiens and benneviaspidiens, of which only the thyestidiens are primarily Silurian. All the Devonian forms are essentially components of the Old Red Sandstone (i.e. non-marine) vertebrate faunas, and were adapted for life in the vigorous, if not highly turbulent, waters of that realm. The development of strong cornual processes was most probably related to life in such a habitat (Janvier 1985*c*). Extended rostra and cornual processes also occur in certain Chinese eugaleaspid (e.g. *Lungmenshanaspis*, see Text-fig. 5). As mentioned above, Janvier (1985*a*, p. 225), like Belles-Isles (1987), considered that in the Boreaspididae the rostral and pectoral processes may have had a dissuasive function against predators such as porolepiforms or arthrodires. The purpose of these long cephalic features is, nevertheless, thought here to be associated not only with locomotion but also with probing or disturbing sediment and vegetation in the search for food.

Osteostracan squamation leads to the view that the trunk and tail were capable of sinuous lateral flexure to a considerable degree, the rigid nature of the scales notwithstanding. Flexure in the vertical plane, however, was probably very limited. The heterocercal tail would have functioned as a large vane moving from side to side to provide a thrust at right angles to itself and contributed a measure of lift. The pectoral fins, set at an angle of incidence to the axis of movement would have carried much of the load in swimming, just as does an aeroplane wing. They would also, as noted above, assist in steering and variable horizontal movement. Thus the cephalaspid, if not all osteostracans, swam by anguilliform motion of the body whereby a wave (movement) progresses backwards through the body to the tail. The speed of the wave along the body is always greater than the speed of the fish through the water. The amplitude of the wave increases as it moves back from head to tail. While the function of the pectoral appendages would have helped to maintain course or steer they would also serve to move the head in a broad sweeping movement from side to side (Belles-Isles 1987, fig. 7). Thus anguilliform movement could be initiated by movement of the head shield, and at the sediment–water interface would disturb organisms and food particles which could then be drawn into the mouth. A rostrum would have effectively disturbed sediment or vegetation forward of the mouth, i.e. normally perhaps upstream, and current activity would move food particles towards the mouth. The disruption of thin algal mats could have been effected by even a small rostrum; the larger rostra could probe filamentous or vascular plant thickets. Examples of rostra capable of this kind of activity are included in Text-figure 5. The question arises as to whether these features be considered as 'advanced' specializations which fitted the animals better to their particular habitat. Long rostra and pectoral cornua arose, as noted above, in several different groups of Devonian agnathans, all associated with the clastic sedimentary facies. Perhaps the possession of these structures offered an advantage such as greater stability when at rest in a habitat founded upon unconsolidated sandy substrates and where frequent shifting of food sites occurred.

It would be interesting to discover if a higher proportion of the cephalaspid in later communities within this facies at Baring Channel possessed extended cornua. The 'community' described here is singular in the relatively large number of cephalaspid individuals it contains. *Ctenaspis* also is common here and appears probably to have had a largely infaunal existence as a detritus feeder. The other vertebrates may also have spent much of their lives as benthos, all being subject to periodic episodes of turbulence and of violent current activity in the water above them.

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